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Keywords:

diversification rates, islands, macroevolution, mountains, speciation, species richness

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Abstract:

Explaining global variation in geographic and taxonomic diversity gradients represents a central focus of macroecology and macroevolution. Ultimately, these diversity gradients have been generated over deep timescales as a consequence of historical variation in rates of dispersal, diversification, and the capacity of different geographic areas to preserve taxa through time. Here, I assess the relationships among these processes, to elucidate the causes of geographic and taxonomic variation in species richness among the most speciose order of birds: the Passeriformes (c. 6,500 species). To achieve this, I comparatively analyze phylogenetic, distributional and eco-morphological trait data collated at broad taxonomic and spatial scales. The results of my analyses strongly support the prevalence of historical dispersal events across large geographic scales, in addition to spatiotemporal variation in diversification rates. These findings reflect that some lineages and some geographic regions (notably tropical mountain regions and

island archipelagoes) generate and maintain a much larger amount of species diversity than others. In addition, the evolution of particular life-history and eco-morphological traits, specifically pair breeding systems, and higher wing aspect-ratios, increased rates of range expansion and diversification. In summary, geographic variation in historical diversification combined with differences in the capacity of lineages to colonize new areas, determines spatial and taxonomic differences in passerine species richness.

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THESIS ABSTRACT

Global dynamics of dispersal and diversification among passerine birds

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Abstract. Explaining global variation in geographic and taxonomic diversity gradients represents a central focus of macroecology and macroevolution. Ultimately, these diversity gradients have been generated over deep timescales as a consequence of historical variation in rates of dispersal, diversification, and the capacity of different geographic areas to preserve taxa through time. Here, I assess the relationships among these processes, to elucidate the causes of geographic and taxonomic variation in species richness among the most speciose order of birds: the Passeriformes (c. 6,500 species). To achieve this, I comparatively analyze phylogenetic, distributional and eco-morphological trait data collated at broad taxonomic and spatial scales. The results of my analyses strongly support the prevalence of historical dispersal events across large geographic scales, in addition to spatiotemporal variation in diversification rates. These findings reflect that some lineages and some geographic regions (notably tropical mountain regions and island archipelagoes) generate and maintain a much larger amount of species diversity than others. In addition, the evolution of particular life-history and eco-morphological traits, specifically pair breeding systems, and higher wing aspect-ratios, increased rates of range expansion and diversification. In summary, geographic variation in historical diversification combined with differences in the capacity of lineages to colonize new areas, determines spatial and taxonomic differences in passerine species richness.

Keywords. Diversification rates, islands, macroevolution, mountains, speciation, species richness.

Introduction

Despite over two centuries of investigation, biologists are yet to comprehensively explain why the distribution and diversity of species varies so much across the world. Although species richness gradients are strongly predicted by energy and water availability (Hawkins et al. 2003) these findings do not alone explain how and where this diversity has been generated (Mittelbach, 2009). Ultimately, the generation of biodiversity must reflect evolutionary history; specifically how rates

of speciation, extinction and dispersal have varied among lineages (Phillimore et al. 2006), through time (Rabosky, 2009), and across space (Jetz et al. 2012). Determining the relative importance of these processes necessitates the study of organismal groups that are variable in their geographic distributions, species diversity, and are relatively well known in respect of their evolutionary relationships. Considering these criteria, passerine birds represent an ideal study group for a number of reasons: (1) they are one of the most species

rich vertebrate orders, having diversified into approximately 6,500 species, (2) these species are very unevenly distributed among the major lineages, (3) species are found across all terrestrial habitats, and the majority of continental and insular landmasses, (4) geographic distributions vary extensively among clades, with some having radiated over large geographic areas, while others are restricted to small habitat patches that extend over only a few km², (5) advances in the phylogenetics and systematics of this radiation are rapidly being made, which in turn is increasing knowledge about their biogeographic history, and (6) extensive study and observation mean that ecological and distributional information are comparatively well known.

I propose and evaluate a hypothesis that potentially explains taxonomic and geographic disparity in passerine species diversity: that geographic variation in opportunities for diversification, combined with the extent to which lineages disperse to and colonize new areas, simultaneously determine the number of species that accumulate among clades and across space. I assess the generality of these relationships among passerine groups, while concurrently attempting to determine their causal factors. My three main research questions were therefore as follows. (1) Is there a consistent relationship between the extent of historical dispersal and diversification? (2) Is there geographic variability in the areas that support lineages which vary in their current rate of diversification? (3) Are there life-history or eco-morphological traits that concurrently account for differences in the propensity for lineages to establish in new areas and radiate there? I address all three questions through the comparative analysis of well-resolved phylogenetic, eco-morphological and distributional data collated across broad geographic and taxonomic scales.

Methods

Phylogenetic, distributional and eco-morphological data

I focused my analyses on two study systems: (1) all passerine birds present within the New World (c. 2,300 species; Kennedy et al. 2014, 2016a), and

(2) the global radiation of Corvids (c. 790 species; Kennedy et al. 2016b,c, Marki et al. 2015). My estimate of the phylogenetic relationships among New World passerine species was obtained from Jetz et al. (2012). For the Corvids, Jønsson et al. (2016) generated a time-calibrated phylogenetic hypothesis for 665 species using Bayesian inference on a DNA supermatrix of up to 10,601 characters (representing four mitochondrial and seven nuclear loci). This phylogeny represents an update of that analyzed in Marki et al. (2015). The remaining species for which sequence data were unavailable at the time of the tree generation were added as polytomies to the phylogeny based on current taxonomy, before using the birth-death model to resolve the polytomies and assign branch lengths (Kuhn et al. 2011). All comparative analyses were performed both on phylogenies that were complete at the species-level, and on those that only considered species with DNA sequence available at the time of the tree generation. Distributional data for the breeding range of all species (both New World passerines and the Corvids) was obtained from an expert-validated database, in which species' ranges were defined from museum specimens, published sightings and more than 1,600 original references (Rahbek et al. 2012). These ranges were recorded at a resolution of 1° x 1° (c. 110 km x 110 km). Ecological (habitat preferences, migratory behaviour), life-history (breeding systems) and further distributional information (presence on islands and continents) were compiled from published literature (see Marki et al. 2015 and Kennedy et al. 2016c for further information). Finally, measurements of primary and secondary wing length were taken for 4,344 museum study skins representing 782 of the 789 species of Corvids recognized by the IOC v.2.7 (Gill and Donsker 2010).

Spatial and phylogenetic comparative analyses

I documented patterns of species richness in 1° x 1° grid cells across different taxonomic scales (order, suborder, infraorder and family) and geographic extents (global, across the New World). My main focus was to assess variation in species diversity among subsets of species that (1) differ

in the extent of their phylogenetic isolation, and hence current diversification rates (Kennedy et al. 2014, 2016a,b), (2) differ in wing morphology (Kennedy et al. 2016c), or (3) differ in breeding system (Marki et al. 2015). These analyses aimed to assess both geographic variation in these diversity patterns, and to locate areas where different groups of species are under or over-represented given the overall richness gradients (e.g., contrasting the diversity patterns of the most phylogenetically isolated lineages with those of the overall clade). Finally, I determined whether differences in diversification rates were related to ecological (habitat preferences, migratory behaviour), morphological (wing morphology), life-history (breeding systems), or distributional (insularity) classifications using phylogenetically corrected regressions (Orme et al. 2013), and trait dependent models of diversification (FitzJohn 2010).

Results

Historical dispersal, diversification and geographic variation in areas supporting lineages that differ in their diversification rates

Among two species rich and broadly distributed groups of passerine birds (all New World passerines and the global radiation of corvoid birds), I found spatiotemporal variation in rates of diversification to be common across lineages. Dispersal and radiation over large geographic areas has not necessarily resulted in heightened diversification (Kennedy et al. 2016a,b). Instead, increased diversification was associated with the colonization of tropical regions that extend over comparatively small areas, but which are topographically heterogeneous and/or fragmented in terms of their landmass connectivity (Kennedy et al. 2014, 2016a,b, Marki et al. 2015; Fig. 1 sections 2-4). Lineages that vary in the extent of their phylogenetic isolation were also consistently found to be maintained in different geographic areas (Kennedy et al. 2014, 2016a,b). For example, tropical mountain regions and island archipelagoes frequently have an overrepresentation of species in the most derived phylogenetic lineages, while tropical mountain regions are also notably diverse in the most phylogenetically isolated lineages (Kennedy et al. 2014, 2016a,b).

Life-history and eco-morphological traits that account for differences in establishment and diversification

Evolutionary changes in breeding systems (the evolution of pair breeding) and wing morphology (the evolution of more projected wing tips/higher aspect-ratios), were correlated with geographic expansion and the increased diversification of passerine clades (Marki et al. 2015, Kennedy et al. 2016c; Fig. 1 sections 1-2 and 4). These patterns reflect the association of the aforementioned trait combinations with increased rates of lineage dispersal and diversification throughout island settings (Marki et al. 2015, Kennedy et al. 2016c).

Discussion

Despite increasingly sophisticated documentation of the geographic and taxonomic variation in passerine species diversity, biologists are yet to provide a complete explanation of these patterns. Further progress in this endeavor necessitates improved understanding about their underlying causal processes: dispersal, diversification, and the preservation of lineages over deep timescales. I assessed factors that determine temporal and geographic variation in these processes among predominantly large clades of passerine birds. One of the most consistent insights emerging from my work is that range expansion and the colonization of new geographic areas promotes lineage diversification, which in many cases has facilitated extensive radiation (Kennedy et al. 2014, 2016a,b, Marki et al. 2015). Clades that have undergone considerable diversification have in many cases also accumulated large numbers of co-occurring species at smaller spatial scales (Kennedy et al. 2016a). These patterns reflect spatiotemporal variation in the diversification process, such that some geographic areas have produced, preserved and currently support a much greater amount of species diversity than others (Kennedy et al. 2014, 2016a,b,c, Marki et al. 2015). Determining why tropical mountain regions (Kennedy et al. 2014, 2016b) and island archipelagoes (Marki et al. 2015, Kennedy et al. 2016c) are so notable for facilitating extensive lineage diversification and preservation requires further appre-

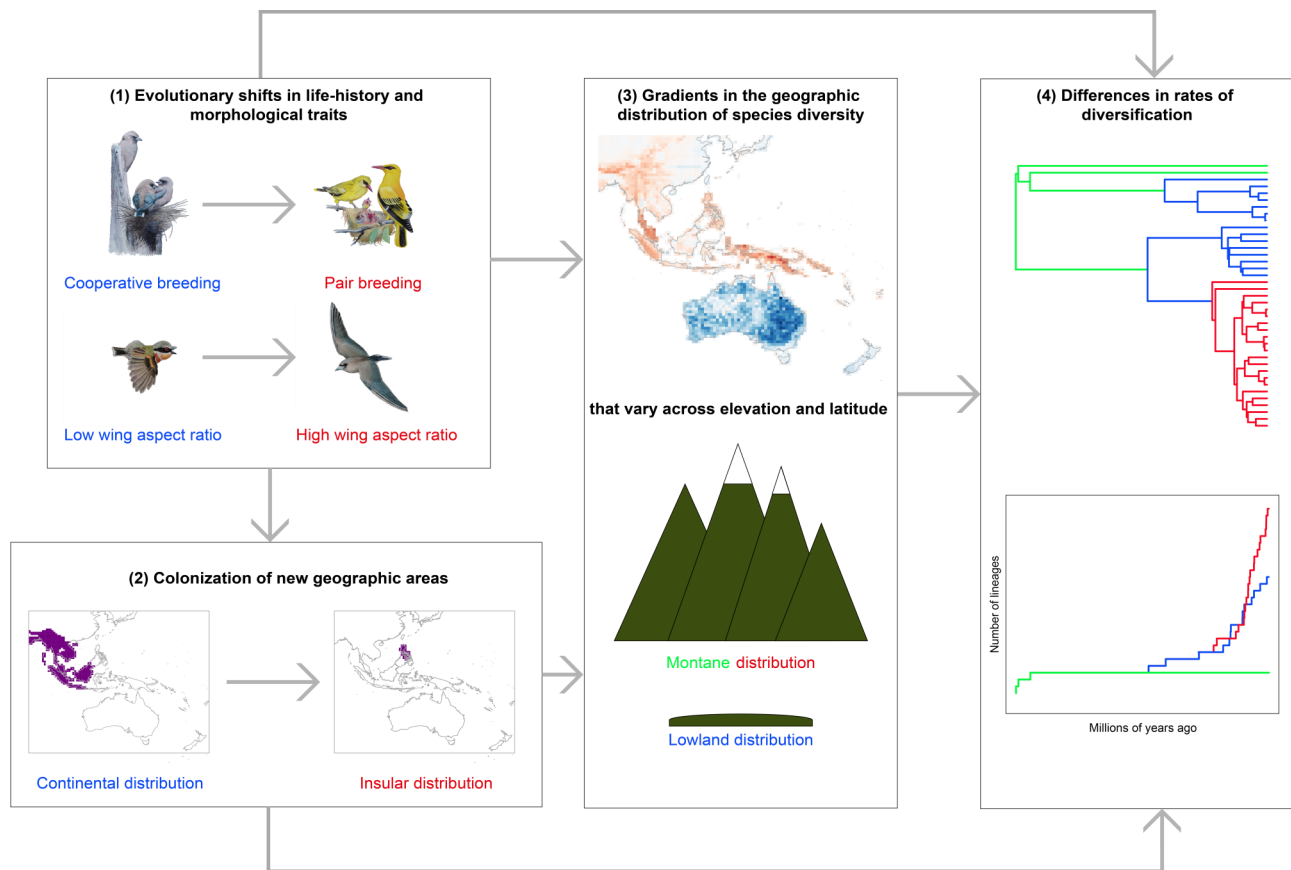


Figure 1. General dynamics of dispersal and diversification among passerine birds. (1) Evolutionary shifts from cooperative breeding to pair breeding and from wings with low to high aspect ratios simultaneously result in (2) range expansion and the colonization of new geographic areas and (3) spatial gradients in the geographic distribution of species. These factors lead to different rates of diversification among passerine clades (4). The geographic distributions, life-history and morphological traits highlighted in either red, blue or green are reflected by the diversification dynamics presented in the same colour on the phylogeny and LTT plot in (4). Jon Fjeldså kindly provided all illustrations.

ciation of the influence that historical changes in geography and climate have had upon these processes (Fjeldså et al. 2012).

Why some passerine lineages disperse and radiate extensively, yet others are more restricted in their geographic occurrence and have accumulated species diversity to a lesser degree, has been poorly understood. My analyses demonstrate that rates of lineage diversification correlate with life-history traits (Marki et al. 2015), morphology (Kennedy et al. 2016c) and insularity (Marki et al. 2015, Kennedy et al. 2016c). Together these factors account for historical differences in phylogenetic expansion among passerine lineages, supporting the idea that changes in geographic distributions, diversification rates, and species traits, are all influenced by common ecological and evolutionary drivers (Fig. 1). Although this implies the potential existence of a unified explanation for the

taxonomic and spatial variation in passerine species richness, improved determination of the specific properties that facilitate or retard geographic and phylogenetic expansion is imperative. Identifying these factors will require the continued generation and refinement of phylogenetic, distributional and eco-morphological trait data, across broad geographic and taxonomic scales. Particular focus should be given to tropical areas in this endeavor, given that this is where species richness is highest, but current data most deficient. However, a potentially greater need is the development of more sophisticated methods to estimate diversification rates, in addition to models that simultaneously assess the influence of historical changes in geographic distributions and phenotypic evolution upon the diversification process. Furthermore, the development of more detailed knowledge about historical climatic stability at local scales could in

congruence with the model development proposed, aid in informing us how populations persist in the hotspots of biodiversity over deep time-scales. Finally, to elucidate any general dynamic, we should avoid focusing so exclusively on the factors that lead some groups to undergo extensive geographic expansion and diversification, but also on those that result in the generation and preservation of range restricted, phylogenetically isolated and species poor lineages.

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